



Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at <http://about.jstor.org/participate-jstor/individuals/early-journal-content>.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.

THE
BOTANICAL GAZETTE

APRIL 1911

ALTERATIONS IN HEREDITY INDUCED BY OVARIAL
TREATMENTS

D. T. MACDOUGAL

(WITH PLATES XIV-XVI AND THREE FIGURES)

During the course of an extended series of experimental cultures of the mutants of the *Oenotheras* and of a large number of other evening primroses native to America, the author conceived the idea early in 1905 that agencies of any kind which might affect the processes of the protoplasts concerned directly in the development of the embryo sac and the differentiation of the egg, and which inhibited or altered the reaction velocities of any process, whether catalytic or otherwise, might cause some alteration in the characters transmitted to the progeny arising from fertilizations into which had entered elements affected in this way.

Brief announcements of the progress of the investigation have been made from time to time, as indicated by the appended bibliography, but it has been deemed advisable to present a résumé of the entire subject, which should include a description of the technique and character of the plants employed, together with the results of the culture of the affected species through a number of generations. It may as well be stated in advance that the earlier conclusions, that the sum of hereditary characters in pedigreed lines of plants may be altered by solutions applied to the ovaries in the stage immediately preceding fertilization, are confirmed by the extended work on the matter, and that one of the earliest derivatives secured in this manner has been carried to the fifth generation without showing indications of returning to the parental type.

The original purpose was to test the matter of localization of the supposed alterations by which discontinuous variations occur in hereditary lines, a matter to which attention was directed by the suggestion of DEVRIES that mutations as exemplified by the derivatives of the *oenotheras* were consequent upon changes in the germ-plasm ensuing previous to the reduction divisions, and, if such localization were established, it was hoped that new mutations might be induced experimentally by controlled conditions or reagents.

As has been pointed out recently, CHARLES DARWIN had attempted to induce alterations in leaves by the injection of reagents which might have acted after the manner of the substances to which galls are due, but this effort was unknown to me, and it may be stated that no results of any kind were secured by him (6).

The announcement of the preliminary results to be described here brought out the information that various workers had placed the bases of excised inflorescences and branches in solutions in the effort to cause embryogenic alterations, and also that specialized water cultures had been used, but without result.

The initial tests were so planned as to include the introduction of solutions into the ovary at a time when pollen and egg were in the stage immediately preceding fertilization. Two plants were chosen for the first trial: *Oenothera biennis*, the form known to American botanists as growing wild under that name; and *Raimannia odorata*, native to Patagonia, and now distributed about the world. Pure-bred material of both species, which had been guarded from possible intercrossing since its introduction into the cultures, was available. Thousands of individuals of many generations of both plants had been cultivated, and in no single instance has anything beyond the well known forms of fluctuating variability been shown, except when diseased plants were encountered. Better authenticated material would be difficult to procure, although, as was proven later, the mechanical conditions offered by the reproductive apparatus of these plants were of such character as not to facilitate the treatment.

It was realized very quickly, however, that the use of the

methods might secure some evidence of value in its bearing upon the influence of environic factors upon germ and soma and their inheritance. This aspect of the matter has taken on an increasing importance, and a score of workers are now busily engaged in experimental inquiries by various methods for the purpose of securing evidence on this subject.

An announcement had been made earlier that *O. biennis* was in a state of mutation, but the cultivation of a second generation demonstrated that the changes under observation were due to a fungal infection (1).

The first series of reagents used were selected for the reason that they might withdraw water from the protoplasts or, by permeating the membranes, exercise a stimulative or inhibitive action upon some of the features of cell action. A 10 per cent sugar solution, solutions of zinc sulphate in distilled water varying from 1 to 10,000, and calcium nitrate 1-1000, constituted the first lot of reagents. These compounds were injected into the ovaries of the plants named during the forenoon of the day at the close of which pollinations would take place, and within 24 hours of fertilization. Every precaution was taken to prevent intercrossing by guarding the inflorescences both before and after the treatments.

A common hypodermic syringe was used, and no more than a portion of a minute drop remained within the densely packed structures of these ovaries, although other plants have since been operated upon which were capable of receiving a large fraction of a cc. of the reagent. With the refinement of technic, operations are now performed with syringes in which a plunger of ground glass is ground into the barrel of a hard glass syringe, to which are attachable needles of 14k gold, by a friction tip which permits thorough cleaning. Solutions are made up in non-sol glass and kept in flasks of the same material.

In the case of the evening primroses, the tip of the needle was thrust into the ovary in a line at an acute angle with its main axis, and as a gentle pressure was applied to the plunger, the needle was gradually withdrawn. Examinations disclosed the fact that many of the ovarian structures were destroyed, the larger number

were totally unaffected, while the reagent would come into contact with a good number in such manner that it might or might not penetrate to the egg apparatus. The shock of the operation is sufficient to cause the entire ovary to be cast off in many species, and for these the method was devised later of using vapors and gases, such as bromine. The surviving ovaries were allowed to ripen in the usual manner, and the seeds duly sowed in pans of fine soil which had been sterilized in an autoclave for several hours. Singularly gratifying results were obtained from these first two plants.

The first experimental test was made with *Raimannia*. Sixteen seedlings were secured, some from ovaries treated with sugar solution, others from ovaries injected with zinc sulphate, and others with calcium nitrate, which were identical in their general characters, being, first of all, annuals in contrast with the bienniality of the parent. This entailed, of course, the continuous formation of elongated internodes from the start, the development of rosettes being due to a stage in stem formation in which the internodes are not separable by external measurements. The cycle of stem formation was therefore a simple curve, starting with a minimum for the seedling, waxing to a maximum, then decreasing with the formation of flowers in the terminal portions, in contrast with the parent, in which the curve is nearly flat for the first season, coming to zero at its end, then rising and falling as in the derivative.

Another feature no less striking was that of the glabrosity of the derivatives, the villous and ciliary hairs of the parent being wholly lacking, no trichomes whatever being formed, these plants being the only evening primroses lacking epidermal extrusions. A number of the second generation were grown, but the third generation was not brought to maturity by reason of incidents attendant upon my removal to the Desert Laboratory in 1906.

The results obtained with *Oenothera biennis* were much more conclusive, and have been followed in such manner as to leave but little doubt as to the nature and character of the changes induced. Among the seedlings grown from seeds produced by ovaries treated with a zinc solution, early in 1906, was one (erroneously given as

two in other publications) that was distinguishable as soon as the cotyledons had attained full expansion, these organs being broader and of a more vivid green, which was also characteristic of the leaves of the rosette. The plants were kept under close observation until maturity, and guarded seeds were obtained. Every

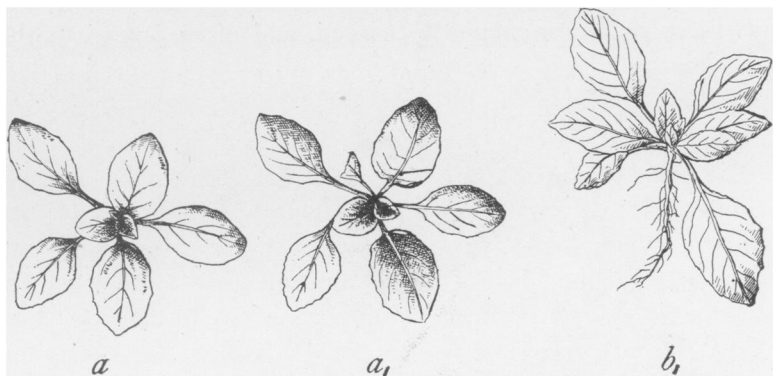


FIG. 1.—*a*, *a*, Rosettes of induced derivatives of *Oenothera biennis* three months old; *b*, rosette of *O. biennis* of same age.

stage of their ontogeny was characterized by features which allowed them to be readily distinguishable from the parent. Successive generations were cultivated in the New York Botanical Garden, in the open, under lath shelters, in glass houses, and at the high mountain plantation of the Desert Laboratory, as well as at the Acclimatization Laboratory, Carmel, California, the close of the fifth generation now having been reached, with no diminution of the degree of divergence by which the new form was first recognized. (See figs. 1 and 2.)

The following formal descriptions were prepared from plants grown in New York under conditions as nearly identical as it was possible to secure them:

OENOTHERA BIENNIS, average form.

Mature rosette.—Leaves ample, rather copiously fine pubescent, the larger ones about 27 cm. long, 6–7 cm. wide; blades oblong to elliptic, or slightly broadened upward, unevenly repand-denticulate and most rather jagged toothed near the base, the petioles relatively stout.

Adult plant.—Plant luxuriant, mostly 1 m. tall or less; stem slightly uneven, but scarcely channeled, hirsute with spreading-ascending somewhat rigid hairs, copiously branched throughout, the lower branches decumbent, the upper ones spreading or curved upward; leaves very numerous, 1.5–2 dm. long near the base of the stem; blades elliptic-ob lanceolate to elliptic-lanceolate; shallowly but rather prominently toothed, and often jagged toothed

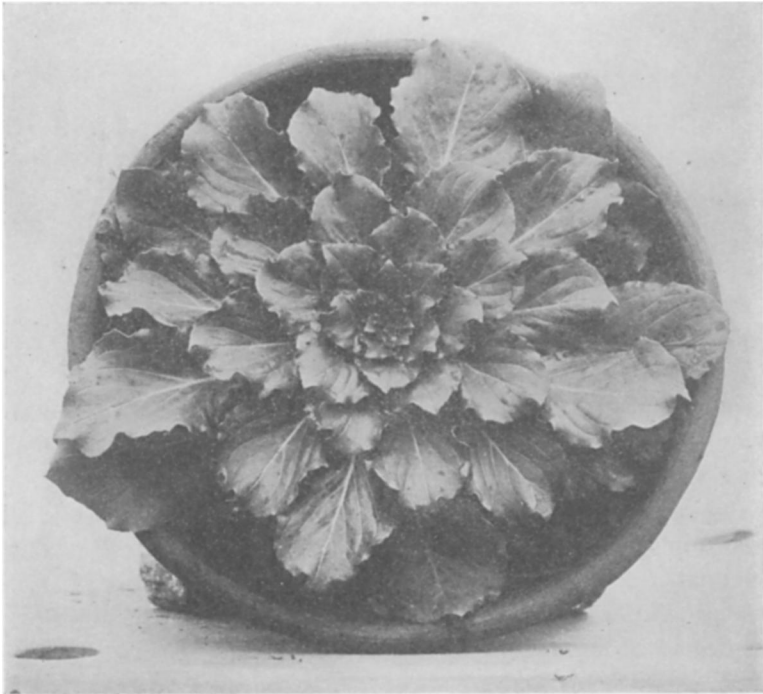


FIG. 2.—Rosette of induced derivative of *O. biennis* five months old; compare with pl. 3, Publ. no. 24, Carnegie Institution of Washington. 1906.

near the base, acuminate, those of the upper cauline leaves mostly elliptic, acute, sessile, or nearly so; bracts mainly lanceolate, narrowed or rounded at the base; conic portion of the bud 14–18 mm. long, finely pubescent, the free tips of the sepals about 2 mm. long; hypanthium 2–3 cm. long, 5–6 mm. wide at the mouth, nearly terete, sparingly pubescent or glabrate; sepals 15–20 mm.

long, much shorter than the tubular portion of the hypanthium, the free tips 4-5 mm. long; petals rather delicate, 12-16 mm. long, truncate or slightly emarginate at the apex; filaments 8-10 mm. long; anthers 7-8 mm. long; pistil shorter than the stamens; stigmas 4-5 mm. long; capsule 3-3.5 cm. long, 7-7.5 mm. in diameter at the thickest point, finely pubescent, slightly curved, markedly narrowed at the apex.¹

It is to be seen from the above description that *O. biennis* is capable of self-fertilization by reason of the superior length of the stamens, a fact that was demonstrated in the experimental grounds. To secure purely fertilized seeds, it was only necessary to inclose the inflorescence in a parchment bag during the opening of the flowers.

DERIVATIVE.

Mature rosette.—Rosette 20 cm. or more in diameter, flat and quite symmetrical; leaves 9-13 cm. long; blades broadest above the middle, 3-3.5 cm. wide, dark green and shining above, pale beneath, minutely pubescent on veins, some of mid veins reddish above, more or less irregularly and sharply denticulate to quite near the base of the margined petioles, margins wavy, undulate, apex of the leaf somewhat twisted.

Adult plant.—Main stem 60-75 cm. high; stem stout, reddish, somewhat angled, minutely appressed-pubescent, interspersed with somewhat larger spreading cilia; branches starting from base of plant all the way up to top, numerous, 10-15 cm. long; stem leaves 7-10 cm. long, oblong-lanceolate, broadest about the middle, 2-3 cm. wide, bright green, shining above, paler beneath, and pubescent on veins, irregularly and sharply denticulate and somewhat wavy margined; bracts varying from oblong to lanceolate, those of lower branches oblong, acute, 1.5-2 cm. wide, those of upper branches 3-4 cm. long, narrowly lanceolate, acute, shining, and glabrate. (See plates XIV-XVI.)

The transference of the parent and derivative to various localities mentioned has resulted in some exceedingly interesting reactions in which fundamental differences have been displayed. In New York and Tucson, the derivative has wider leaves of a more

¹ Publication no. 24, Carnegie Institution of Washington. 1905.

vivid green than the parent, giving an effect of greater luxuriance. The derivative endures the climate of the mountain plantation better than the parent. In both places the derivative uniformly exhibits a greater amount of red in the leaves than the parent. At Carmel the reddish color is accompanied by a yellowish tinge, the green of the parent remaining practically unchanged. The parent is characterized by an excessive development of the basal

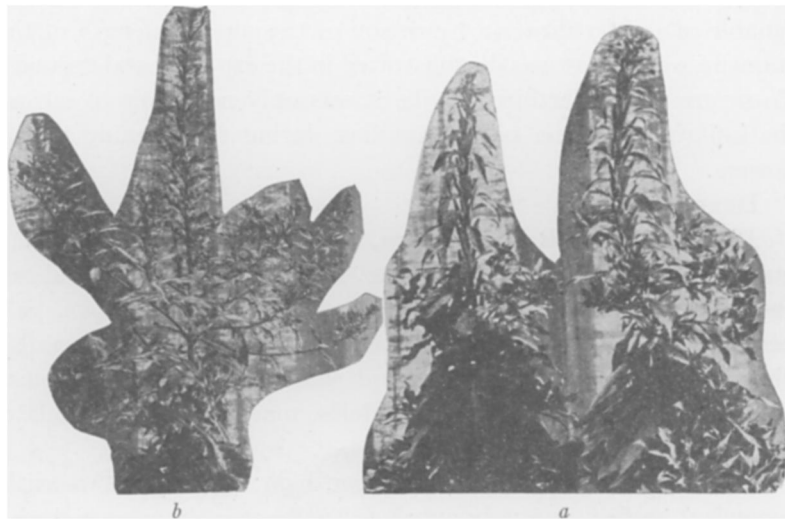


FIG. 3.—*a*, Flowering shoots of *O. biennis*, with broad leaves and short heavy upper branches, grown in equable climate of Carmel, California; *b*, flowering shoot of induced derivative, with narrow leaves and long slender uppermost branches, grown at Carmel.

branches at this place, which are heavy, robust, very leafy, and terminated by dense broad rosettes or by inflorescences. Here, as elsewhere, the capsules are longer than those of the derivative (see pls. XV and XVI) and are more noticeably angled. The derivative grown at Carmel bears numerous branches, which are longer above than in the parent, and are more ascendant, terminating in dense tufts of small reddish bractlike leaves or inflorescences. The capsules of the derivative at Carmel are generally few-seeded. This may be ascribed to the fact that the pistils here are generally longer than the stamens and are exerted from the bud, thus preventing

self-fertilization. The derivative is thus seen to differ from the parent in every stage of ontogeny and reproduction. The differences in question have been maintained through five generations and four sets of climatic and soil conditions.

A few hybridizations of derivatives with the parent have been made; with the result that the cross is found to be intermediate, being more vigorous and showing greater leaf-development than either parent, features which are also displayed in the second generation. The entire set of structural and physiological differences, together with the results of the cross with the parent, points to the conclusion that the derivative is a genotype different from that of the parental form, to which, of course, it stands most closely allied, but with which it does not intergrade.

The successes with these two forms inspired an extended range of experiments with a number of species of widely diversified morphological type, principally characteristic of the arid regions, from 1906 to the present time. Among these were included *Eschscholtzia*, *Argemone*, *Physalis*, *Covillea*, *Carnegiea*, *Mentzelia*, *Opuntia*, *Anemone*, *Amsinckia*, *Pentstemon*, *Echinocereus*, *Echinocactus*, *Sphaeralcea*, *Nicotiana*, *Fouqueria*, *Solanum*, *Kallstroemia*, *Mimulus*, *Phytolacca*, and *Brodiaea*. In addition, diligent watch has been kept for ovaries in which the stings of insects made at an early stage have resulted in serious malformations, with the view of testing probable action upon ovules contained. Only one set of seeds has been secured in this manner so far, and no deviations from the normal were found in the progeny arising from them.

In 1910 some new methods of treatment were tested, by which vapors of various substances, including bromine, were allowed to act upon inclosed inflorescences with eggs and ovules in various stages of development. The fatalities were large, but several progenies from this treatment are now under observation. Practically all plants were grown as they had become established naturally, and no effort was made to secure pollination except in one or two instances in *Pentstemon*. The proportion of losses from various causes was large in all cases. Operations were fairly successful in *Pentstemon*, but the stalks bearing ripening capsules were

harvested so completely by rock squirrels that, out of the hundreds on the slopes near the laboratory, only two or three were allowed to stand in place until the seeds were escaping from the capsules. The three surviving treated stalks of this plant that were saved were preserved by wrapping the stems in cloth. The losses in *Eschscholtzia* were very great, by reason of the quick response of this plant to injuries. *Echinocereus* failed to set a single fruit that had been treated during the first year, although quantities of seeds from treated ovaries have since been secured. Several dozens of ripening capsules of *Argemone* were destroyed by birds; *Mentzelia* matures but few seeds in each capsule; *Opuntia* fails to set fruits in many cases, owing to the injurious effects of the operation and failure to pollinate. *Carnegiea gigantea* drops many flowers that have been operated upon and fails to pollinate many, so that not more than 12 or 15 per cent of the operations were successful with this plant.

These data concerning the fatalities encountered are of interest, since they deal with plants wholly in a state of nature, and represent with fair measure the chance of survival in similar cases that might occur without human intervention.

Some attention has already been given to the conditions found in *Pentstemon Wrightii*, a small beard-tongue native to southern Arizona. This plant displays a wide range of variability in its various habitats. The plants treated on Tumamoc Hill, however, are restricted in the range of somatic characters, their progeny from treated ovaries displaying many supposedly new qualities. A most diligent observation has been made of the wild plants to distinguish naturally recurring characters from those induced. It now seems fairly certain that some new characters are found in the treated progenies. The actual examination of these forms is fraught with great difficulty, since it has not been found possible to secure fertilization in guarded inflorescences, due probably to the fact that the action of visiting insects has not been correctly imitated.

It is evident that the operations described above entail the introduction of reagents into the complex ovular mechanism, and no rational interpretation would be possible without an analysis of

the behavior of the fluid and its possible contact with the main or accessory reproductive elements. First of all, it is important to determine whether the solutions affect the egg cells or the pollen elements, and a number of tests were made with dyes for this purpose. The large ovaries of the giant cactus (*Carnegiea gigantea*) offered some excellent opportunities for testing these points.

The introduction of reagents into the ovaries of this plant was accomplished by thrusting the tip of a needle of a syringe diagonally downward into the cavity through the wall, and then by a steady pressure of the plunger perhaps as much as 0.4 to 0.6 cc. of solution was forced in, setting up a pressure that in some instances increased the external dimensions of the ovary, and the withdrawal of the needle was often followed by the ejection of some of the fluid, but the high turgidity of the walls soon closed the aperture or perforation.

The flowers of *Carnegiea gigantea* ordinarily open in the morning and attract a variety of bees and small gnats, the former probably being instrumental in pollination. Plants taken to the New York Botanical Garden in 1902 did not set seeds unless pollinated by hand. The flowers open in the morning and close with the day when the temperature is above 80° F., but on cooler or cloudy days the flowers may remain open during a part or all of a second day.

The style is as much as 5 or 6 cm. in length, and the pollen tube arising from grains falling on the stigmatic surfaces seems to take nearly a day in effecting fertilization, although exact observations on this point could not be made. It was deemed best, therefore, to inject solutions into the ovaries at any time between 10 A.M. and 4 P.M., thus securing the possibility of affecting the egg apparatus, or the pollen tube as it advanced.

The introduction of methyl blue at this time was followed by its absorption by the inner walls of the locule, and its conduction to the apex of the ovarian cavity at the base of the style in such manner that entering pollen tubes must pass through the impregnated layer, and would be subject to the action of free coloring agent, whether traveling intracellularly or intercellularly. That

it was colored was proved by examination of material a day later, when many stained filaments could be seen. Beside this, the stain was taken up by the concave flanks of the ultimate placental branches which were stained very deeply, and which by their conductive action carried a large quantity of the reagent into the ovule, where it spread between the outer and inner integuments, but it was separated from the nearest portion of the egg apparatus by several layers of cells. Micropylar structures were stained but sparingly when the reagent was introduced into the bases of opening flowers as above.

If, however, the injection was made on the day previous to the opening of the flower or earlier, the placental stalks were not stained so deeply, the amount introduced into the ovule being very small or mostly none at all. On the other hand, the inner integument at the micropylar orifice was deeply stained, so that any pollen tube entering through this structure would certainly encounter the reagent. The conducting tissue on the inner surface of the locule was deeply stained at this stage, and by its action much of the color was conducted to the apical region through which the pollen tube must pass.

It is to be seen, therefore, that the placental stalk presents a concave flank most highly absorbent and conductive at the time that the egg apparatus is complete and awaiting fertilization. Before this time, the introduction of a reagent results in greater affection of the endostome and greater accumulation of the coloring matter in the basal portion of the pistil through which the pollen tubes must pass. The probabilities would be greatly in favor of a reagent acting upon the pollen nucleus when introduced at this stage, to the total exclusion of any direct effect upon the embryo sac. Injections on the day of fertilization, at a time when most of the successful operations were performed, resulted in some of the solution going into the ovular structures, but not into such close contiguity that the embryo sac might be supposed to be affected. In a few instances the endostome was also stained, while the tissue through which the pollen tubes pass into the locule accumulated the reagent.

Oenotheras were injected with methyl blue at the Desert

Laboratory in June 1907 to ascertain the probable mechanical effects by which divergent derivatives had been induced in two genera. Colored solutions introduced into the ovaries the day before fertilization showed but meager effect in comparison with the actual results of injection in the cactuses. The stain was found adhering to the outer layers of the ovule, in which the embryo sac lay deeply buried. In no instance was anything like a marked penetration observed. The placental stalks were stained in a few instances, and rather deeply, and this offers the only shadow of a clue as to possible effects of the introduced reagents. The number of ovules affected in any way well accords with the comparatively meager effects secured. It was noted also that the rupturing of the ovarial walls freed numbers of crystals of calcium carbonate, which were partly dissolved by many of the reagents and would thus complicate hypothetical reactions.

The introduction of methyl blue solutions into ovaries of *Mammillaria* on the days the flowers were opened, resulted in staining the papillar cells which project from the sharp angles of the funicular or placental stalk, which is curved in such manner that a pollen tube would pass among them, probably coming into the closest contact with their mucilaginous walls. Here, as in *Carnegiea*, the introduction of a foreign substance would place the greatest chance of affection of the germinal elements within the pollen tube. Further tests were made with a solution obtained by allowing powdered carmine to stand in distilled water. The introduction of the reagent into the ovaries of the flowers that had opened was followed by a general absorption of it by the absorptive cells of the concave flanks of the funicular stalks, and by the underlying cells, with only a slight affection of the ovule and only an occasional reaction from endostomes. Injections of flowers the day before opening, however, gave more marked results. In this case, not only was the dye taken up by the conductive systems lining the locules as in the case above, but the stain had traveled up the base of the pistil for as much as a centimeter. Furthermore, the reagent was not only taken up in quantity by the funicular stalk, but it had been conducted into the ovule, where much of it had accumulated between the outer and inner integu-

ments. Beyond this it could not be traced, although it seems reasonable to suppose that some action extended beyond. At the same time, numerous endostomes could be detected which had taken on a marked stain. Not only were the external cells colored, but the action extended inward some distance.

The study of the movements of dyes yields some profitable suggestions as to the probable mechanical movements of reagents introduced into ovaries for the purpose of affecting the egg apparatus or the pollen tube. The coloring matter was not seen to penetrate farther than a point separated by five or six protoplasts from the egg nucleus. The pollen tube carrying the fertilizing nucleus, however, may be compelled to pass through or among cells taking up any foreign substance, so that only the two walls and the cytoplasm intervened. It seems, therefore, that the greater weight of probability lies on the side that the proembryonic affection of the germinal elements of a seed plant is one in which the possible changes are to be supposed to be due to the action of the reagent on the pollen nucleus rather than on the embryo sac.

The care of treated plants until the seeds in treated ovaries have matured and may be harvested has absorbed much effort, since in many species the plants may ripen a few seeds daily, and collections must be made frequently. Next after the harvesting of the seeds, sowings must be made at the proper time of the year. In the case of species of the desert it has not been found profitable to attempt germinations except at the customary time, else enormous fatalities may occur. Many of the forms which offer particularly favorable conditions for ovarian treatments are slowly developing perennials, which need several years to reach the stage in which they may produce seeds and thus furnish a second generation.

At the present time, seedlings from treated ovaries are under observation as follows: *Echinocereus Fendleri*, *Echinocactus Wislizeni*, *Brodiaea capitata*, *Fouqueria splendens*, *Sphaeralcea pedata*, *Pentstemon Wrightii*, *Phytolacca decandra*, *Opuntia discata*, *Carnegiea gigantea*, *Amsinckia spectabilis*, and *Solanum eleaegni-folium*. Of these, lots from successive seasons are under observa-

tion from two species, in which some species are represented by two or more different treatments.

The announcement was made in 1908 that some divergent characters were seen in a treated progeny of *Cereus*. The plant in question, by the incessant changes of nomenclature, is known at the time of this writing as *Echinocereus Fendleri*. The progeny is coming into bloom, and while one of the individuals diverges widely beyond the observed range of fluctuating variability, it cannot yet be definitely stated whether or not the characters displayed are permanently heritable or not. The individual in which they are represented is of normal vigor, and is not in any ordinary sense monstrous or teratological.

It may be readily apprehended that any theoretical interpretation of the action of the reagents employed in this series of experiments is extremely difficult. The question as to whether the embryo sac or the generative nucleus of the pollen tube is acted upon is, withal, a purely mechanical consideration. The real problem is the nature of the alterations induced by the action of the compounds to which the test plants are subjected.

Some of the earlier results with *Raimannia* were obtained with solutions of cane sugar, not of tested purity, however, and applied with built-up metal syringes, and corrosion may have occurred to such an extent as to make the action similar to that in which solutions of metals and halogens were used in proportions of 1 to 10,000 or 1 to 50,000 of distilled water. The application of zinc and iodine solutions in the more carefully guarded operations may have affected the reproductive protoplasts in various ways. The chief difficulties in the way of theoretical interpretations consist in the fact that the direct action of the reagents cannot be followed in the deeply buried reproductive elements. It can only be said that the reagents might alter the dissociations in the cell, while not entering it, or perhaps only in the minutest quantities, and the properties of an egg might well diverge with changes in the relative number of free ions of various kinds in its compounds. This assumes, of course, a direct connection between the chemical constitution of the cell and the properties it displays. The entire effect might be due simply to altered

permeability of the limiting membranes of the protoplasts or of the vacuolar sacs.

Experimental studies such as are here described lead the investigator into the consideration of two phases of the subject. One is concerned with the demonstration of induced hereditary alterations and the study of their behavior in pedigreed strains, in hybridizations, and under various environic conditions. The other includes a consideration of the mechanism by which an environic agency affects the physical bearers of heredity. Both comprise some important and interesting possibilities in evolutionary science.

DESERT LABORATORY
TUCSON, ARIZONA

EARLIER PAPERS BY THE AUTHOR ON RESULTS OF OVARIAL TREATMENTS

1. Heredity and the origin of species. *Monist*, Jan. 1906; reprinted in advance Dec. 1905, and as Contribution No. 80 of the New York Botanical Garden, 1906.
2. Heredity and environic forces. Vice-presidential address before Section G, A.A.A.S., at Chicago meeting, Dec. 30, 1908; reprinted in advance of annual volume.
3. Heredity and the origin of species. Smithsonian report for 1908, pp. 505-523; issued in 1909.
4. Physiology of genetics. Sixth year book, Carnegie Institution of Washington, p. 62, 1907; seventh year book, p. 63, 1908.
5. Alterations in heredity induced by ovarial treatment. Eighth year book, Carnegie Institution of Washington, p. 59, 1910.
6. The direct influence of environment. Fifty years of Darwinism, p. 114, 1908.
7. Origination of self-generating matter and the influence of aridity upon its evolutionary development. Outlines of geologic history, by WILLIS and SALISBURY, p. 278, 1910.
8. Environic response. *Amer. Nat.*, Jan. 1911; also *Science*, Jan. 20, 1911.

EXPLANATION OF PLATES XIV-XVI

PLATE XIV.—*A*, rosette of *Oenothera biennis* at Desert Laboratory, 1910; *B*, rosette of induced derivative.

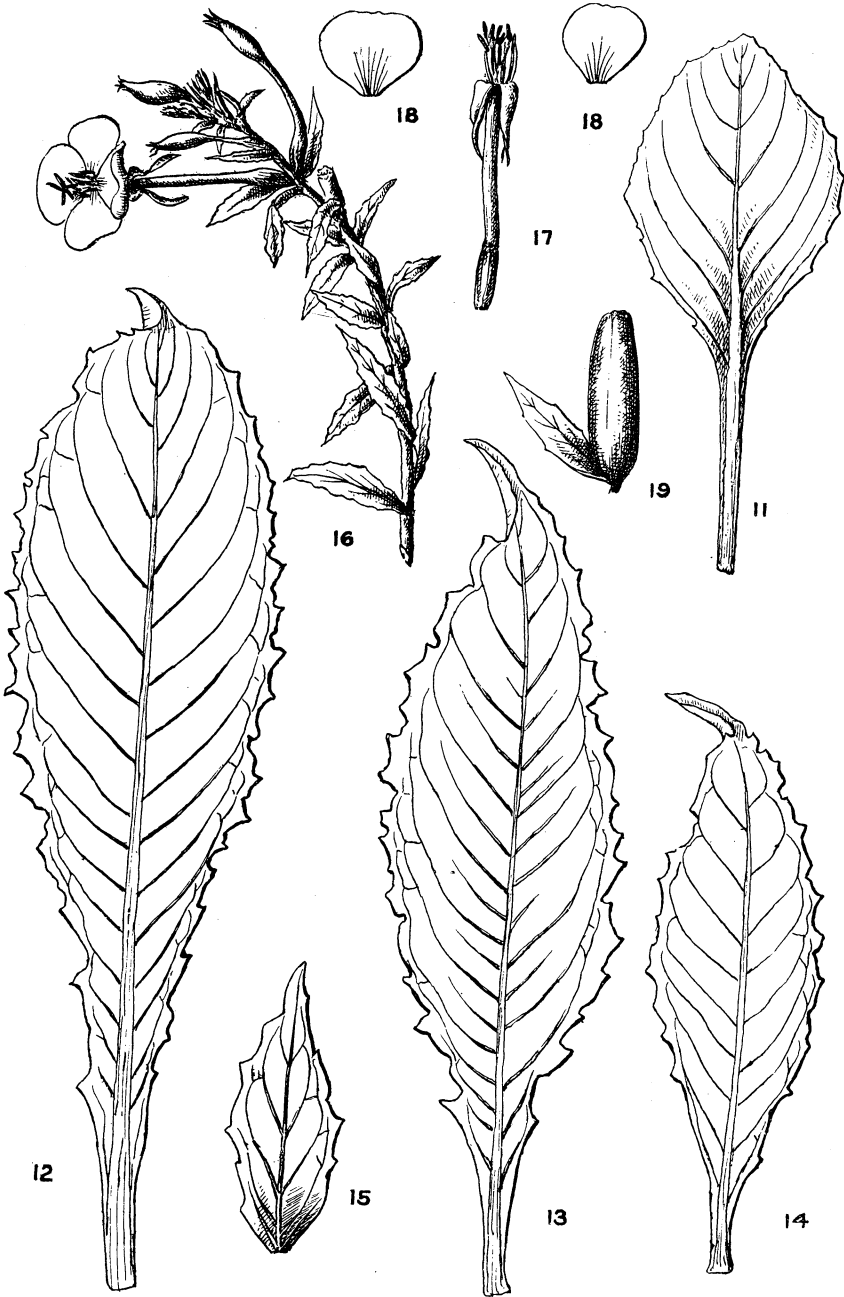
PLATE XV.—*Oenothera biennis*: 1, leaf from young rosette; 2, leaf from rosette four months old; 3, leaf from lower part of mature rosette; 4, leaf



MACDOUGAL on OVARIAL TREATMENTS



MACDOUGAL on OVARIAL TREATMENTS



MACDOUGAL on OVARIAL TREATMENTS

from upper part of mature rosette; 5, stem leaf; 6, bract; 7, unopened bud; 8, flower with petals removed; 9, petals of maximum size; 10, mature capsule; 1-5, one-half natural size; 6-10, natural size.—From Publ. no. 24, Carnegie Institution of Washington. 1905.

PLATE XVI.—Derivative of *Oenothera biennis*: 11, leaf of young rosette; 12, leaf from mature rosette; 13, leaf from mid-stem; 14, leaf from upper part of stem; 15, bract; 16, flowering branch; 17, flower stripped of corolla; 18, petals; 19, capsule and bract.